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THE IDENTITY AND STATUS OF SPIRANTHES OCHROLEUCA (RYDBERG) RYDBERG¹

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Spiranthes is taxonomically the most complex orchid genus in the flora of eastern North America. Within the genus, some of the greatest problems center on *S. cernua* (L.) L. C. Rich., a very poorly understood species which has been the recurrent victim of both splitters and lumpers for over one hundred years. A number of segregates have been proposed; these subsequently have been accorded various taxonomic ranks, relegated to synonymy, or forgotten altogether. One such taxon, *Gyrostachys ochroleuca* Rydberg, was described in 1901 (Rydberg, *In*: Britton, 1901, p. 300) and has been the object of controversy ever since.

The original description of *Gyrostachys ochroleuca* provided few points of difference from the description of *G. cernua* in the same publication. Rydberg's species was reported to bear leaves on the lower portion of the stem similar to the basal leaves, and lanceolate to ovate-lanceolate acuminate floral bracts, the lower of which were longer than the flowers. The flowers were described as ochroleucous or greenish-yellow and strongly fragrant. In contrast, in *G. cernua* cauline leaves were reportedly merely bract-like and floral bracts were acute and generally not longer than the flowers. Flowers of *G. cernua* were reported to be white and fragrant. Additionally, the diameter of the spike was given as 15–20 mm for *G. ochroleuca* and 12–14 mm for *G. cernua*. The key preceding the description separated *G. ochroleuca* from *G. cernua* on the basis of yellow

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flowers, acute spike, and lower floral bracts longer than the flowers. The description ended: "Otherwise as in *G. cernua*," and gave the distribution as "N.H. to N. Car., and Penn." Rydberg dismissed typification of *G. ochroleuca* with the phrase, "Type from Mt. Washington, Mass.," and a type specimen is unknown.

Ames (1905) early reduced *Gyrostachys ochroleuca* to varietal status under *Spiranthes cernua*. Later he (Ames, 1921) commented on the near impossibility of separating the two taxa and stated that the only reliable difference known to him was the presence of polyembryonic seeds in var. *cernua* and of monoembryonic seeds in var. *ochroleuca*. Since that time, authors of various manuals of the northeastern flora and regional studies of the Orchidaceae have treated it as a variety, a separate species, or have omitted it altogether, either considering it part of the variation of *S. cernua* and unworthy of recognition, or being unable to identify it with certainty in the area covered. Ames (1924), referring to *ochroleuca* as a variety, extended its range into Nova Scotia and included "Mo. (Palmer)." Rydberg (1932) retained its specific rank, transferring it to *Spiranthes*, and expanded its range to most of the eastern United States, from Maine to Georgia and west to South Dakota and Texas.

Swamy (1948), in a detailed study of the embryogenesis of the group, showed that polyembryony in *Spiranthes cernua* was a consequence of agamospermy. He recognized a strictly apomictic race marked by the production of polyembryonic seeds, a sexual race exhibiting solely monoembryonic seeds, and a facultatively apomictic "intermediate" race in which both sexually produced monoembryonic and apomictically derived polyembryonic seeds were characteristically developed in the same capsule. He failed to mention var. *ochroleuca*, but wrote, "unfortunately no reliable characters in gross morphology are known which would help to segregate the sexual and agamospermic races;" this suggests that he was influenced by Ames' (1921) statement concerning the seeds. Swamy indicated a very widespread eastern North American distribution for the polyembryonic, asexual race, a more limited and sporadic occurrence of the "intermediates", and a restricted northeastern range for the monoembryonic, sexual race. Much of the material upon which he based his initial work was obtained from Ames, and consequently it is reasonable to conclude that his agamospermic races correspond to *S. cernua* var. *cernua* and the



Figure 1. Type drawing of *Spiranthes ochroleuca* at NY labelled "*Gyrostachys ochroleuca* Rydb. ined. Britton's Manual 1901. Drawings by Mrs. Long, Mt. Washington, Mass. 1897."

strictly sexual race to *S. cernua* var. *ochroleuca*, as understood by Ames. If this conclusion is correct, the range reported by Swamy was certainly contrary to that reported by Rydberg (1932) who should have known the plant best; however, Swamy's map was based on 5,000 herbarium specimens representing 28 states!

Correll (1950) did not treat var. *ochroleuca* separately, but alluded to it briefly as an upland form with yellowish-tinged flowers and longer floral bracts in his treatment of *Spiranthes cernua* var. *odorata* (Nutt.) Correll. He also indicated that it was separated primarily on the basis of its monoembryonic seeds, and commented further: "to the average individual such ultratechnical characters are not readily useable."

Fernald (1950), according *ochroleuca* varietal status under *Spiranthes cernua*, characterized it similarly, but made the significant addition: "Its callosities longer." Longer basal calli in *S. ochroleuca* are shown in the plate provided by Correll (1950, Plate 70) which was earlier used by Ames (1921, Plate 127). Jennings (1906) cited the long calli of specimens from Presque Isle, Lake Erie, as the salient feature separating *Ibidium incurvum* Jennings from *I. cernuum*. He later (1953) reported these specimens to be merely vigorous *S. cernua*, and further indicated the occurrence of long calli in both typical *S. cernua* and *S. cernua* var. *ochroleuca*. Recent authors have overlooked the name *I. incurvum* altogether.

State floras have been equally variable in their treatments of *Spiranthes ochroleuca*. For example, Deam (1940) specifically excluded it from the Indiana flora, although Steyermark (1963) reported it from Missouri, and Barkley (1968) included it in the Kansas flora. Case (1964) reported it from Michigan, but Voss (1972) has not mentioned it from that state. Sheviak (1973) considered this disparity of treatments to be largely a result of the confusion of this taxon with other members of the *S. cernua* complex, and did not (Sheviak, 1974) report it from Illinois.

Most recently Luer (1975) has accorded *ochroleuca* specific rank. Here it was distinguished from *Spiranthes cernua* by its larger incurved basal calli, lesser dilation at the base of the lip, creamy flowers, flowers more widely spaced on the rachis, lip that expands more broadly into a crenulate margin, later flowering time, more restricted distribution, and drier habitat. This characterization of *S. ochroleuca* agrees well with the concept evolved earlier in this



Figure 2. The type of *Spiranthes cernua* (L.) L.C. Rich. (LINN 1056.9).

century. The confusion which has surrounded the taxon, however, suggests that the actual situation is very complex. Luer's recognition of *S. ochroleuca* at the specific level, a decision based primarily on field experience and discussion with local botanists, has both drawn attention to the problem and generated additional questions. This is evident from the repeated requests the authors have received to clarify the matter. Without type material and additional supportive evidence, and considering the nature of the original description, it has been difficult to do so.

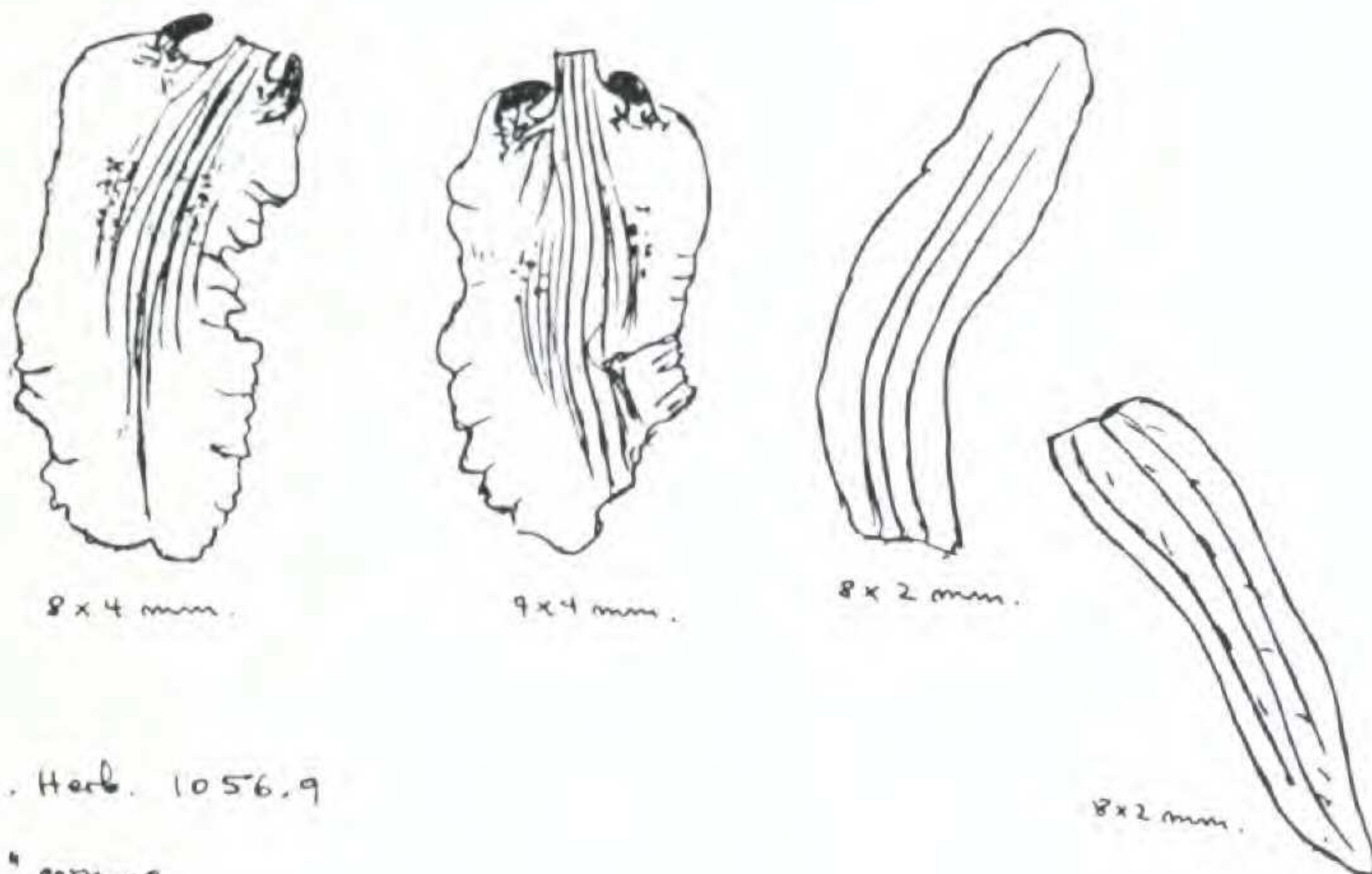
The confusion which has surrounded the application of Rydberg's name has not been limited to difficulties in the separation of *Spiranthes ochroleuca* from *S. cernua*. In the Midwest, *S. ochroleuca* has been confused with *S. magnicamporum* Sheviak (Sheviak, 1973). *Spiranthes ochroleuca* is also sometimes confused with *S. casei* Catling and Cruise (Catling & Cruise, 1974). Most recently, Luer (1975) has compared *S. ochroleuca* to *S. laciniata* (Small) Ames.

It is clear that both the taxonomic status and identity of *Spiranthes ochroleuca* have been problems, and indeed continue to be. The present authors independently came to recognize the same group of plants as *S. ochroleuca* and became convinced of its distinctness. A number of questions persist, however. What are the distinctions in both qualitative and quantitative terms? Can the species be discriminated on the basis of morphology alone, and to what extent can herbarium material be discriminated? Do the names presently in use correctly apply to the taxa they are taken to represent? What is the actual distribution? Is specific status justified?

METHODS

1. General survey of natural populations

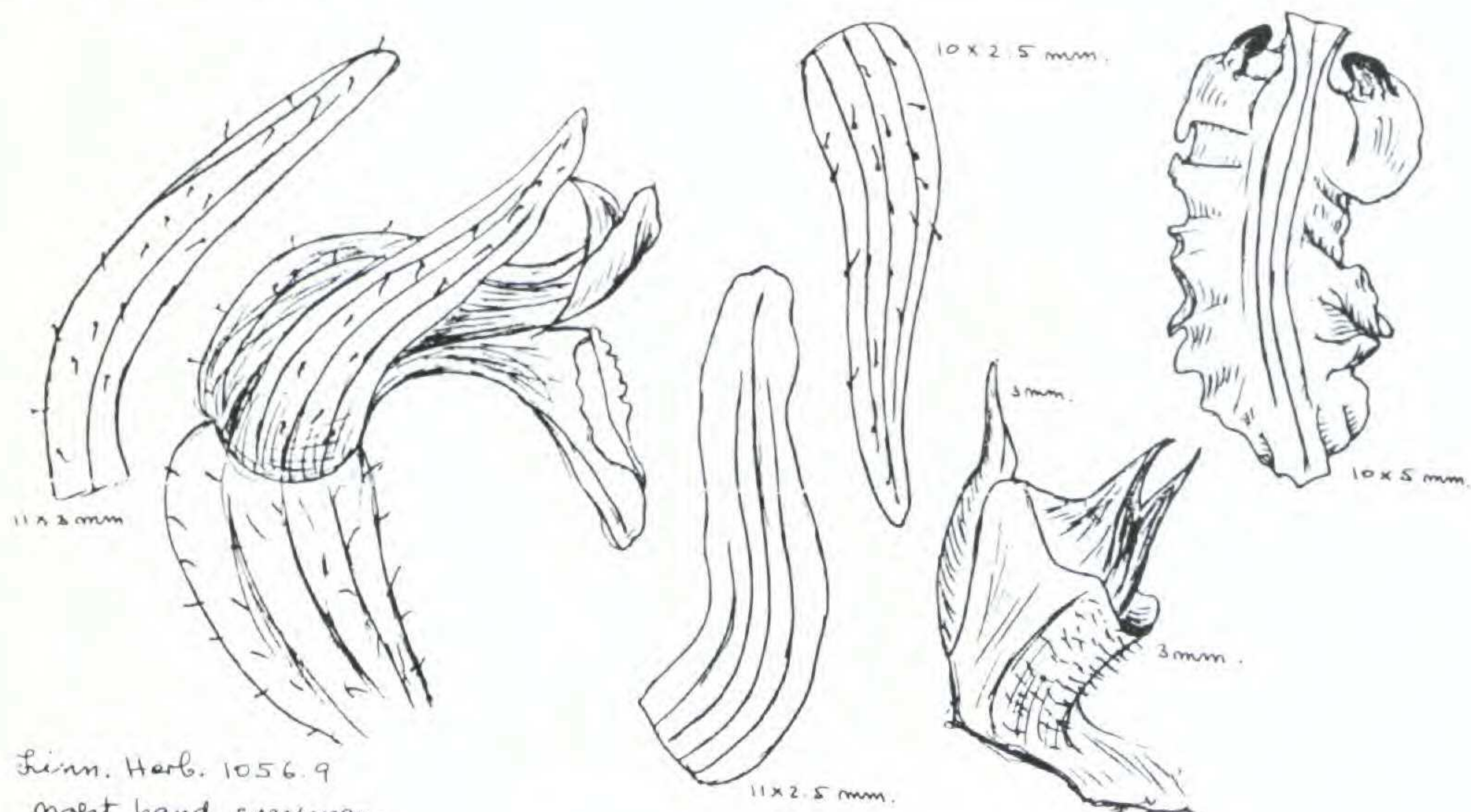
Notes were made on flower colour, flowering time, habitat, and distinctive features in colonies over a wide geographical area extending from New England to southwestern Ontario. Special attention was given to localities where *Spiranthes ochroleuca* and *S. cernua* grew in close proximity. One such area is the type locality of *S. ochroleuca*: Mt. Washington, Mass. Here populations referable to *S. ochroleuca* and *S. cernua* were studied in detail to allow for accurate redescription.

Ophrys cernua Linn.

Linn. Herb. 1056.9

"4" cernua

left hand specimen

Ophrys cernua Linn.

Linn. Herb. 1056.9

right hand specimen

Figure 3. Camera lucida drawings of flowers from the type material of *S. cernua* (LINN 1056.9) made by Dr. L. A. Garay. Above, left hand specimen, from left to right, lip 8×4 mm, lip 7×4 mm, petal 8×2 mm, lateral sepal 8×2 mm. Below, right hand specimen, from left to right, lateral sepal 11×3 mm, flower in lateral view, petal 11×2.5 mm, lateral sepal 10×2.5 mm, column 3 mm with anther sac 3 mm and lip 10×5 mm.

Plants photographed and/or measured in the wild were grown under uniform greenhouse conditions (soil, light, moisture, and temperature). This allowed for a test of the extent to which various presumably characteristic features are modified by the environment.

In order to evaluate the features of floral morphology that separate *Spiranthes ochroleuca* from *S. cernua*, and in an attempt to find additional features, 20 flowers of each taxon pickled in standard FAA fixative were examined closely. These had been collected by the authors throughout the northeast. Camera lucida drawings were made to illustrate the salient differences. As well as providing illustrations, this examination allowed the selection of characters to be used in the statistical analyses described below.

2. Herbarium studies

Since a large part of the difficulty in determining the application of the name *Spiranthes ochroleuca* results from the apparent absence of type material, extensive herbarium searches were conducted in an effort to locate a specimen seen by Rydberg. The collection of the New York Botanical Garden (NY), where many of Rydberg's types are located, was searched intensively. In addition, the collections of several other herbaria were examined; these included AMES, CAN, CM, DAO, F, ILL, KANU, MICH, MIL, MIN, NDA, NEBC, NYS, OKL, OKLA, PENN, PH, TRT, US, VDB, WIS, and others. These herbaria provided the specimens of *S. ochroleuca* which formed the basis of our range map.

3. Cytological studies

Chromosome counts were obtained from over sixty individuals collected throughout the range of the *Spiranthes cernua* complex. Chromosome number determinations were made primarily on somatic tissue. Complex pairing in some polyploids and small chromosome size precluded the general use of meiotic figures for counting. Tissues utilized included root tips from pot-grown plants and ovules from both cultivated and collected material. Root tips and ovaries were deeply incised and then placed in a saturated aqueous solution of monobromonaphthalene for four hours at 18–24°C. or overnight on ice. They were then fixed in Carnoy's solution for about 25 minutes before storage in 70% ethanol at ca. –15°C. or squashing. Root tips and ovaries were hydrolyzed in 1 N. HCl at 55–60°C. for 8 to 15 minutes and stained with acetolacmoid.

Chromosome numbers and seed characteristics, which have been found to correlate with ploidy level (Sheviak, unpubl.), were studied throughout the range of *Spiranthes cernua*. To a lesser extent, pollen characters were also examined. Attempts were made to correlate these features with other characters. Some of the material for which chromosome numbers had been determined was used in the statistical analysis (see below).

4. Statistical analysis of flower morphology

As mentioned previously, plants referable to *Spiranthes ochroleuca* and *S. cernua* were found in abundance at the type locality, Mt. Washington, Mass. Here 22 flowers of each species were collected for measurement. In addition three flowers were collected from plants that could not be readily assigned to either species, but appeared in the field more like *S. cernua*. These were labeled "intermediate". Each flower was collected from the basal portion of the inflorescence of a different plant, and all flowers were pickled in standard FAA. Twenty-four measurements made on each of these flowers are listed in Table 1.

Some of the measurements require explanation. The method of measurement of the separation of dorsal and lateral sepals (1), the angle of curvature of the lip from the basal stalk (8), and the angle of basal curvature of the lip (22) are illustrated in Figure 4. The aperture (5) refers to the aperture formed at the base of the lip by the lip, the basal lateral petal, and the top of the ovary, and is apparent in the lateral view of the flower with the lateral sepal removed (Figure 6). The length and width of the basal calli (16) refers to the mean length and mean basal width, respectively, of the two structures on a single lip. The lateral width of the anther sac (18) refers to its width as viewed from the side, while the dorsal width (24) refers to the width as viewed from above. The basal and middle lateral widths of the flower (6 and 7, respectively) are widths measured 1 mm from the base and at the midpoint along the length of the flower respectively, with the lateral sepal removed and viewing the flower from the side.

The numerical taxonomy system of multivariate statistical programs (NT-SYS) written by F. J. Rohlf, J. Kishpaugh and D. Kirk (1974, State University of New York, Stony Brook) was used to produce a character-by-character correlation matrix based on standardized data. This correlation matrix involving 24 characters

Table 1. Units, means, standard deviations and character weights for 24 floral characters measured in 22 pickled flowers of *S. ochroleuca* and 22 of *S. cernua*, all from the type locality, Mt. Washington, Massachusetts, OCHR=*S. ochroleuca*, CERN=*S. cernua*.* To the discriminant function add the constant 0.720.

Character	Units	Means		Standard Deviations		DFA Character Weights*
		OCHR	CERN	OCHR	CERN	
1. Separation of sepals	mm	0.9	0.5	0.3	0.2	—
2. Sepal length	mm	8.8	8.8	0.7	0.5	—
3. Sepal width	mm	2.6	2.7	0.3	0.2	—
4. Length of aperture	mm	0.8	0.6	0.1	0.2	—
5. Width of aperture	mm	0.6	0.4	0.1	0.1	—
6. Basal lateral width of flower	mm	3.4	3.1	0.3	0.3	—
7. Middle lateral width of flower	mm	2.7	2.7	0.2	0.3	—
8. Angle of curvature of lip from basal stalk	°	55.8	31.0	9.9	11.0	0.051
9. Petal length	mm	9.5	9.0	0.7	0.6	—
10. Petal width	mm	2.2	2.5	0.2	0.2	—4.677
11. Dorsal sepal length	mm	9.5	9.2	0.8	0.5	—
12. Dorsal sepal width	mm	3.2	3.0	0.3	0.2	—
13. Lip length	mm	9.2	8.9	0.7	0.5	—
14. Maximum lip width	mm	4.8	4.8	0.5	0.5	1.460
15. Length of basal calli	mm	1.2	0.9	0.2	0.1	3.621
16. Width of basal calli	mm	0.8	0.8	0.2	0.2	—
17. Length of anther sac	mm	2.2	2.4	0.1	0.2	—8.528
18. Width of anther sac (lateral)	mm	1.0	0.8	0.1	0.1	12.215
19. Length of stigmatic surface	mm	1.3	1.1	0.2	0.1	—
20. Width of stigmatic surface	mm	1.7	1.8	0.2	0.1	—
21. Column length	mm	3.9	3.6	0.4	0.3	1.616
22. Angle of basal curvature of lip	°	46.3	22.2	8.9	15.5	—
23. Length of disc (rostellum)	mm	1.5	1.5	0.1	0.1	—
24. Width of anther sac (dorsal)	mm	1.2	1.1	0.1	0.2	—

(see Table 1) was subjected to a Principal Components Analysis. In this procedure individuals are ordered along uncorrelated axes, while variation in all characters among all the individuals is considered simultaneously (Sneath & Sokal, 1973, pp. 245–247). Any major groupings in the sample data are elucidated through this technique.

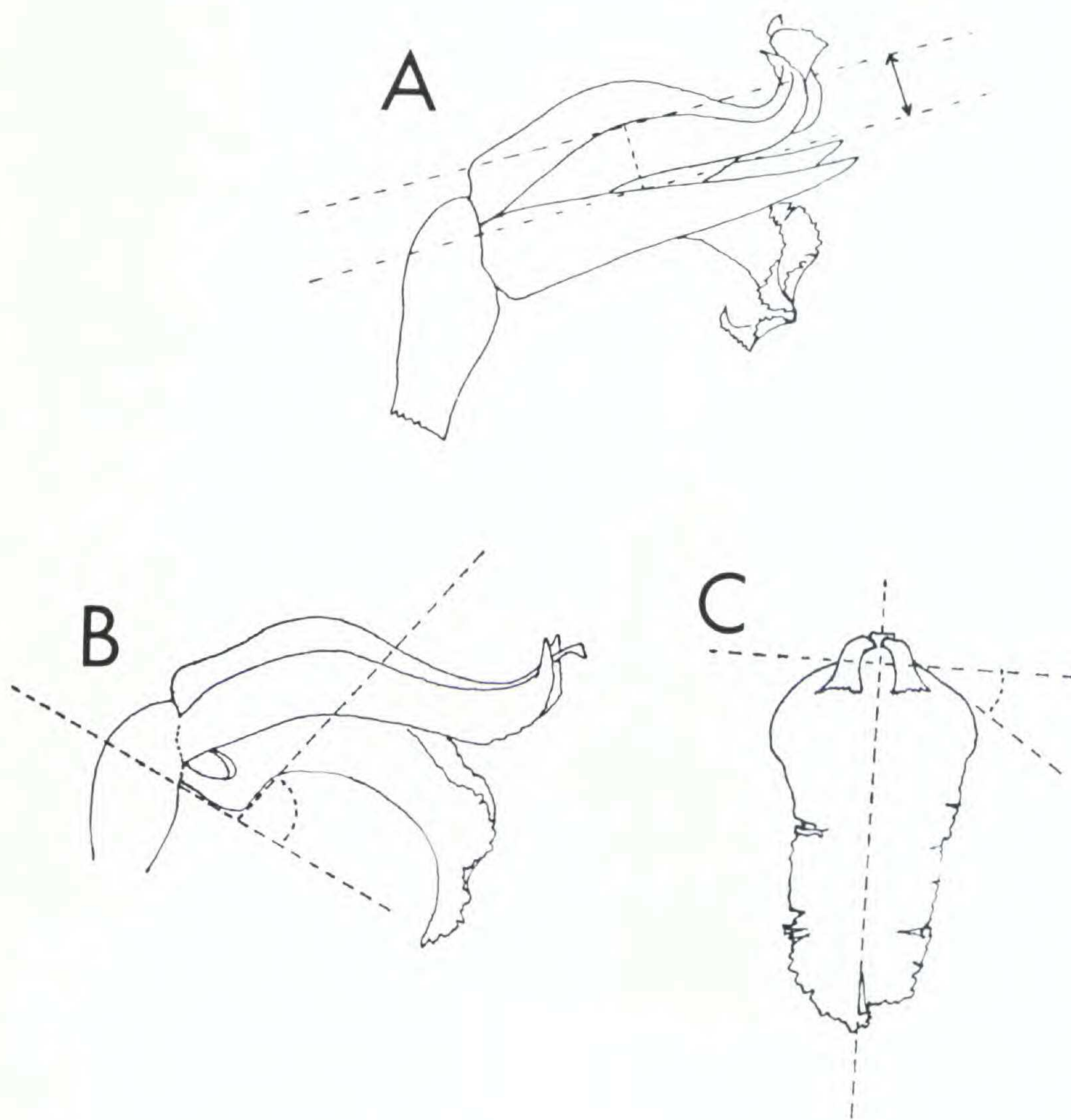


Figure 4. Method of measurement of A, separation of dorsal and lateral sepal; B, the angle of curvature of the lip from the basal stalk; and C, the angle of basal curvature of the lip.

A stepwise Discriminant Function Analysis program (BMDP 7M) developed by P. Sampson (1975, University of California, Los Angeles) was used to maximize discrimination between identifiable groups. This multivariate procedure maximizes intergroup differences with respect to intragroup differences through the development of weighted character combinations. The discriminant scores for each specimen are obtained by multiplying each measurement by the appropriate discriminant weight and adding the resulting values. Unknowns may be identified by applying the weighted character combination (see Table 1) derived from the DFA reference samples, the latter representing specimens of known affinity. Multivariate statistical programs were run on the University of Toronto IBM/370 computer.

5. Statistical analysis of dried material

In addition to a statistical treatment of flowers from the type locality, it was thought that a statistical analysis of dried material covering a wide geographical area would help to elucidate further the nature and variation of *Spiranthes ochroleuca*, and assist in the development of means for the determination of herbarium specimens with an acceptable misdetermination rate.

For this analysis dried material collected by the authors and known to be referable to either *Spiranthes ochroleuca* or *S. cernua* on the basis of flower colour, habitat, and various qualitative features was chosen for measurement. For some of this material chromosome numbers were also known (Table 3). Eleven measurements were made of each of 30 individuals of *S. ochroleuca*; 37 of *S. cernua*; and two of specimens, from mixed populations, which could not be readily determined. The collection localities and corresponding number of specimens of each group measured are given in Table 3; the characters, units of measurement, means and standard deviations are shown in Table 2. Various type material was also considered in these analyses. The angle of ascension of the flower (7) refers to an angle measured from a line perpendicular to the main axis of the plant. Again, all floral measurements refer exclusively to basal flowers. The same statistical techniques and programs were employed for the analysis of dried specimen data as for the study of flower morphology described above.

Table 2. Units, means, standard deviations, and character weights for 11 characters measured in 30 dried specimens referable to *S. ochroleuca* and 37 referable to *S. cernua*, representing a wide geographical area of the northeast. OCHR = *S. ochroleuca*, CERN = *S. cernua*. *From the first discriminant function subtract the constant 4.362 and from the second subtract 3.589.

Character	Units	Means		Standard Deviations		DFA Character Weights*	
		OCHR	CERN	OCHR	CERN	1	2
1. Length mid-stem bract	mm	49.3	33.5	15.4	7.6	0.017	0.027
2. Length of spike	mm	83.0	58.3	35.6	23.2	0.024	—
3. Flower number	—	29.0	20.1	9.3	6.6	0.000	—
4. Plant height	mm	264.0	239.3	81.6	60.9	—0.004	—
5. Ovary length	mm	5.2	6.2	0.7	1.2	—0.491	—0.527
6. Separation of lateral and dorsal sepals	mm	0.8	0.3	0.3	0.2	2.425	3.742
7. Angle of ascension of flower from ovary	°	110.7	100.9	11.5	13.7	0.016	—
8. Length lowest floral bract	mm	13.3	11.2	2.7	1.8	0.240	0.297
9. Length lateral sepal	mm	8.3	8.4	0.9	0.9	—0.257	—
10. Width lateral sepal	mm	2.1	2.1	0.3	0.4	0.220	—
11. Basal curvature of lip from basal stalk	°	46.3	15.1	14.4	10.1	0.055	—

Table 3. Subjectively determined categories, number of specimens, chromosome numbers, and collection sites of dried material used in statistical analyses.

	<i>S. ochroleuca</i>	Indet.	<i>S. cernua</i>
ILLINOIS			
Iroquois Co. (<i>Sheviak</i> 699)			1 ($2n=60$)
Will Co. (<i>Sheviak</i> 470)			1 ($2n=60$)
MASSACHUSETTS			
Berkshire Co. (<i>Catling</i> 4 Sept. '75)	1		2
(<i>Sheviak</i> 1076, TOPOTYPE)	2 ($2n=30$)		
(<i>Catling</i> 831c, TOPOTYPE)	10 ($2n=30$)		
(<i>Catling</i> 83a)			5 ($2n=ca.60$)
Middlesex Co. (<i>Sheviak</i> 821)			2 ($2n=ca.60$)
Worcester Co. (<i>Sheviak</i> 891)			2 ($2n=60$)
Worcester Co. (<i>Sheviak</i> 922)			1 ($2n=60$)
MAINE			
Sagadahoc Co. (<i>Sheviak</i> 870)	1 ($2n=30$)		
Sagadahoc Co. (<i>Sheviak</i> 915)	1 ($2n=30$)		
York Co. (<i>Sheviak</i> 888)			2
York Co. (<i>Sheviak</i> 1113)		1 ($2n=45$)	
York Co. (<i>Sheviak</i> 1070)	1		
MICHIGAN			
Saginaw Co. (<i>Gunn</i> 15 Sept. '73)	2		
Saginaw Co. (<i>Sheviak</i> 1065)	1 ($2n=30$)		
Saginaw Co. (<i>Sheviak</i> 1155)			1
NEW HAMPSHIRE			
Belknap Co. (<i>Sheviak</i> 1022)	2 ($2n=30$)		
Cheshire Co. (<i>Sheviak</i> 1041)	1 ($2n=30$)		
Coos Co. (<i>Catling</i> 1 Sept. '76)	1 ($2n=30$)		
Merrimack Co. (<i>Sheviak</i> 875)			2 ($2n=60$)
Sullivan Co. (<i>Sheviak</i> 877)	1 ($2n=30$)		
Sullivan Co. (<i>Sheviak</i> 1063)		1 ($2n=45$)	
Sullivan Co. (<i>Sheviak</i> 1036b)			1 ($2n=61$)
Sullivan Co. (<i>Sheviak</i> 1036g)			1
Sullivan Co. (<i>Sheviak</i> 1035)	1		
Sullivan Co. (<i>Sheviak</i> 1034)			1 ($2n=45$)
NOVA SCOTIA			
Shelburne Co. (<i>Catling</i> 25 Aug. '75)	1		
ONTARIO			
Haliburton Co. (<i>Catling</i> 12 Sept. '71)			1
Kent Co. (<i>Catling</i> 18 Sept. '76)	1		
Muskoka Dist. (<i>Whiting</i> 10 Sept. '70)			1

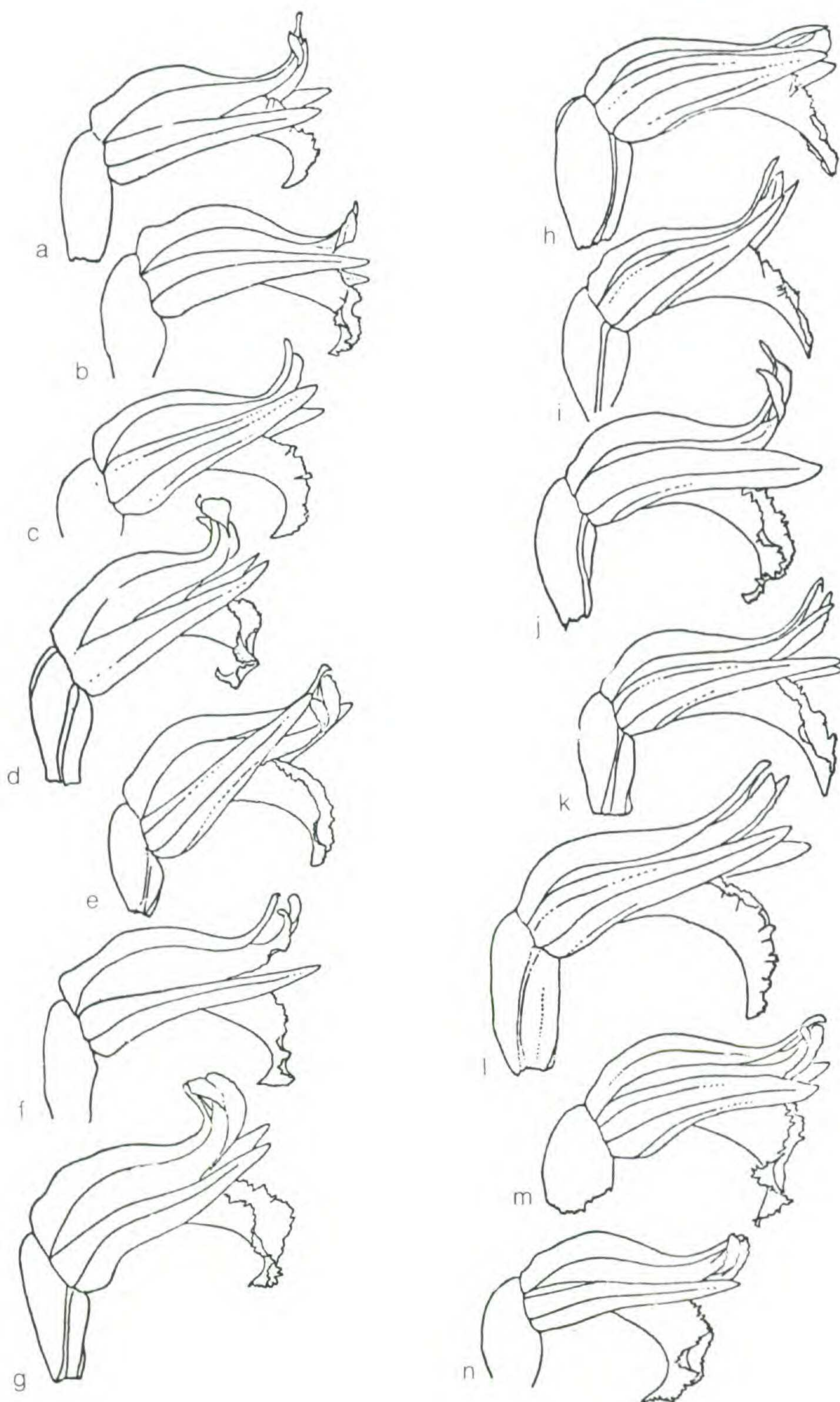
Table 3 continued

Norfolk Co. (TRT 153068)		3
Ontario Co. (Catling 13 Sept. '70)		1
Wentworth Co. (TRT 85372)		1
York Co. (Catling 21 Sept. '72)		1
PENNSYLVANIA		
Bradford Co. (Catling 13 Aug. '76)	1	
Erie Co. (Sheviak 988, <i>I. incurvum</i> , TOPOTYPE)		3
QUEBEC		
Sherbrooke Co. (Catling 5 Sept. '74)		2
VERMONT		
Windham Co. (Sheviak 1043a)		2
Windham Co. (Sheviak 1044)	2	
Number of OTU's		
<i>Spiranthes cernua</i> (including 3 <i>Ibidium incurvum</i> topotypes)		37
<i>S. ochroleuca</i>		30
Indeterminates		2
Total		67

RESULTS AND DISCUSSION

The Types

Citation of the type of *Gyrostachys ochroleuca* has not been made in the literature; it may be significant that Ames, despite his emphasis on proper typification, never mentioned a type. Examination of the collection of the New York Botanical Garden revealed only a single specimen from the type locality old enough to have served as the type of *G. ochroleuca*. This small, poorly preserved specimen (*W. M. Whitfield s.n.*, 30 August 1889) shows no signs of ever having been seen by Rydberg, and is apparently referable to *Spiranthes cernua*. Another collection by Whitfield, made a few days later on 5 September, does appear to represent *S. ochroleuca*; this specimen is in the herbarium of the University of Minnesota (MIN 94418) and similarly cannot be connected with Rydberg.



The New York Botanical Garden collection (NY), however, includes a drawing labeled "*Gyrostachys ochroleuca* Rydberg ined. Britton's Manual 1901. Drawings by Mrs. Long, Mt. Washington, Mass. 1897" (Figure 1). Significantly, an additional series of drawings, also at NY, is labeled "Drawings by Mrs. Long of *Spiranthes cernua*. Mt. Washington, Mass. September 1897." It appears that the drawing labeled *G. ochroleuca* is Rydberg's type. This conclusion, suggested by the labeling of the drawing, is supported by the correlation between the characteristics of the drawing and those attributed to *G. ochroleuca* in Rydberg's description. Additionally, comparison with archival materials indicated a strong possibility that the label is in Rydberg's hand, although a relationship could not be established with certainty.

The drawings of *Spiranthes cernua* illustrate rather well some of the previously suggested distinguishing characteristics of this species, such as nodding flowers and basally dilated lips. In contrast, the drawing of *Gyrostachys ochroleuca* shows a plant with ascending flowers and an ovate-oblong, non-dilated lip. The basis for Rydberg's description of the spike in *G. ochroleuca* as acute is also revealed in this drawing. The larger plant illustrated is in very early flower and, like all northeastern *Spiranthes* in this stage of development, the upper part of the inflorescence is composed of erect pointed buds of decreasing size resulting in an acute tip. The five drawings of *S. cernua* represent plants all fully in flower, and not surprisingly the inflorescences appear obtuse. This is, additionally, a significant early suggestion of a slightly later flowering time for *S. ochroleuca* at the type locality. The lower floral bracts in the

Figure 5. Camera lucida drawings made from pickled flowers of *S. ochroleuca* and *S. cernua*. Flowers viewed laterally.

a-g. *Spiranthes ochroleuca*. a,b,c, Mt. Washington, near Hunts Pond, Berkshire Co., Mass., 10 Sept. 1976. d, 10 miles E of Lee, Berkshire Co., Mass., 4 Sept. 1975. e, 2 miles W of Jordan Falls, Shelburne Co., Nova Scotia, 25 Aug. 1975. f, Armenia Mt., S of Sylvania, Bradford Co., Penn., 10 Sept. 1976. g, 1/2 mile N of Thamesville, Zone Tp., Kent Co., Ont., 18 Sept. 1976.

h-n. *Spiranthes cernua*. h,i, Mt. Washington near Hunts Pond, Berkshire Co., Mass., 10 Sept. 1976. j, 10 miles E of Lee, Berkshire Co., Mass., 4 Sept. 1975. k, Toronto Island, York Co., Ont., 24 Sept. 1976. l, 1 mile SW of Lake St. Nora, Stanhope Tp., Haliburton Co., Ont., 29 Aug. 1976. m, Mont Orford Park, Sherbrooke Co., Quebec, 5 Sept. 1974. n, 1 mile NE of Erroll, Coos Co., New Hampshire, 1 Sept. 1976.

illustration of *G. ochroleuca* are, as described by Rydberg, ovate-lanceolate, acuminate, and longer than the flowers. Those illustrated for *S. cernua*, in contrast, are quite variable, but often shorter than those of *G. ochroleuca* and more ovate, with an aristate, rather than acuminate, apex.

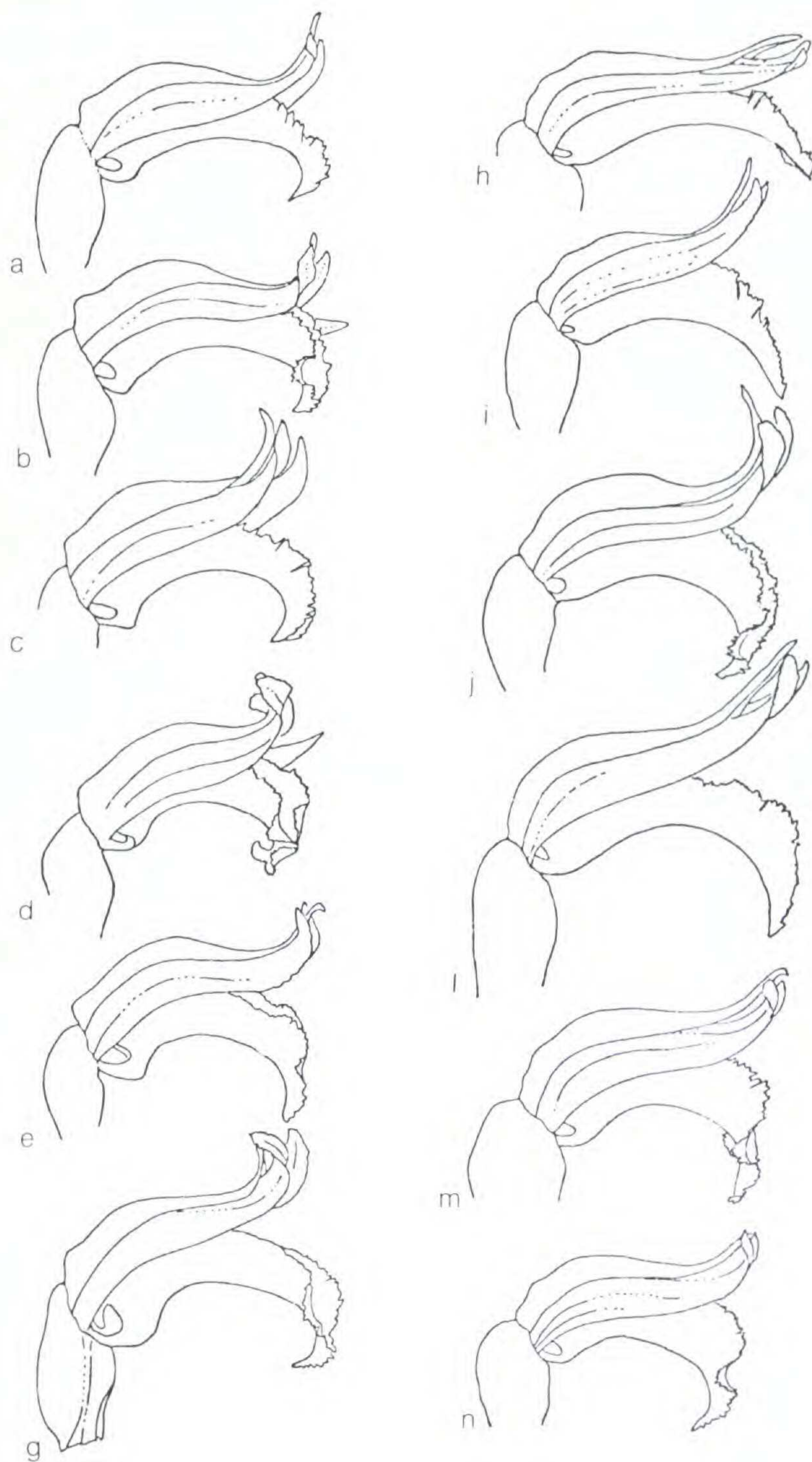
Typification of *Spiranthes cernua* is easily established. In the Linnaean herbarium in London is a specimen (LINN 1056.9: Figure 2) on which Linnaeus has written "*cernua*" and "K" (*i.e.* Kalm). Although Linnaeus did not directly indicate the basis for the description of his new species *Ophrys cernua* in *Species Plantarum* in 1753, he did state "Habitat in Virginia, Canada". Since Linnaeus had Kalm's collection of "Canadian" material prior to 1753, and any reference to Canada by Linnaeus refers exclusively to Kalm's work, a Kalm collection would be a suitable choice for a lectotype. There are two plants on the sheet (LINN 1056.9). The right hand specimen bears a highly characteristic inflorescence of densely arranged, nodding flowers. This specimen does not include roots. The left hand specimen, bearing roots, has a less well developed inflorescence of rather ascending flowers, with only a few nodding flowers interspersed. This condition is found in *S. cernua* when it is grown in dense vegetation, and in cultivation such plants produce inflorescences of horizontal or nodding flowers. Linnaeus' description included reference to both nodding flowers and roots, so we must assume that he based his concept on both of these specimens.

Asa Gray annotated the right hand specimen "*Romanzoviana* A. Gray" and the left hand specimen "*cernua auctor.*" Oakes Ames later wrote on the sheet, "Gray is most certainly mistaken—this is *S. cernua*, Oakes Ames, Nov. 14, 1905." Dr. L. A. Garay has kindly

Figure 6. Camera lucida drawings made from pickled flowers of *S. ochroleuca* and *S. cernua*. Flowers viewed laterally with the lateral sepal removed.

a-g, *Spiranthes ochroleuca*. a,b,c, Mt. Washington, near Hunts Pond, Berkshire Co., Mass., 10 Sept. 1976. d, 10 miles E of Lee, Berkshire Co., Mass., 4 Sept. 1975. e, 2 miles W of Jordan Falls, Shelburne Co., Nova Scotia, 25 Aug. 1975. g, 1/2 mile N of Thamesville, Zone Tp., Kent Co., Ontario, 18 Sept. 1976.

h-n, *Spiranthes cernua*. h,i, Mt. Washington, near Hunts Pond, Berkshire Co., Mass., 10 Sept. 1976. j, 10 miles E of Lee, Berkshire Co., Mass., 4 Sept. 1975. l, 1 mile SW of Lake St. Nora, Stanhope Tp., Haliburton Co., Ontario, 29 Aug. 1976. m, Mont Orford Park, Sherbrook Co., Quebec, 5 Sept. 1974. n, 1 mile NE of Erroll, Coos Co., New Hampshire, 1 Sept. 1976.



provided us with drawings of the flowers from each of these specimens. It is clear from these drawings (Figure 3) that neither plant represents *Spiranthes romanzoffiana*, which is characterized by a pandurate lip.

The measurements accompanying Garay's drawings of the type material enable the length of the calli to be calculated. These calli lengths range from ca. 0.8 to 1.0 mm and are therefore more like *Spiranthes cernua* than *S. ochroleuca* (Table 1). A correlation exists between lip length and calli length; larger lips have larger basal calli. Therefore it is convenient to express the calli length in relation to the lip length. Ratios of the length of the lip to the length of the calli are usually less than 7.5 in yellow-flowered upland plants referable to *S. ochroleuca*, but average 8.0–9.0 in *S. cernua*. The ratios for the three lips illustrated by Garay are ca. 9.0–9.4.

The floral bracts measuring ca. 10.3 mm in the left hand specimen of LINN 1056.9 and ca. 12.5 mm in the right hand specimen are well within the usual range of white-flowered plants generally called *S. cernua*, and the leaves are all basal, the stem bearing only cauline bracts. Therefore the type material of *S. cernua* does not display characteristic features of *S. ochroleuca* as described originally by Rydberg. In fact, LINN 1056.9, which we designate as lectotype of *S. cernua*, clearly represents the taxon treated as *S. cernua* by recent American authors.

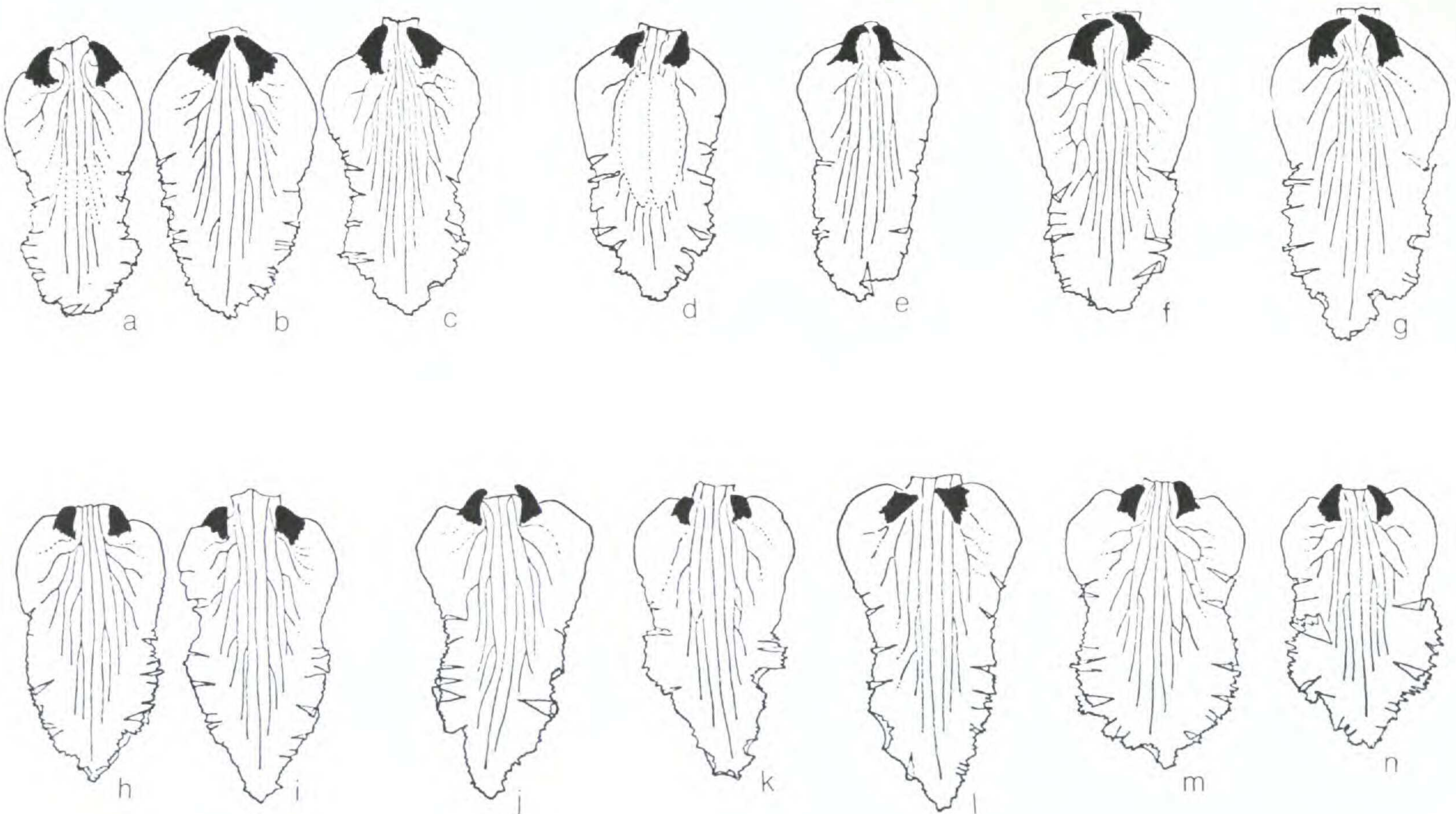
The type locality

Yellow-flowered plants in drier sites referable to *Spiranthes ochroleuca* and white-flowered plants of more moist habitats

Figure 7. Camera lucida drawings made from pickled flowers of *S. ochroleuca*. Upper surface of lip pressed flat.

a-g. *Spiranthes ochroleuca*. a,b,c, Mt. Washington, near Hunts Pond, Berkshire Co., Mass., 10 Sept. 1976. d, 10 miles E of Lee, Berkshire Co., Mass., 4 Sept. 1975. e, 2 miles W of Jordan Falls, Shelburne Co., Nova Scotia, 25 Aug. 1975. f, Armenia Mt., S of Sylvania, Bradford Co., Penn., 10 Sept. 1976. g, 1/2 mile N of Thamesville, Zone Tp., Kent Co., Ont., 18 Sept. 1976.

h-n. *Spiranthes cernua*. h,i, Mt. Washington, near Hunts Pond, Berkshire Co., Mass., 10 Sept. 1976. j, 10 miles E of Lee, Berkshire Co., Mass., 4 Sept. 1975. k, Toronto Island, York Co., Ont., 24 Sept. 1976. l, 1 mile SW of Lake St. Nora, Stanhope Tp., Haliburton Co., Ont., 29 Aug. 1976. m, Mont Orford park, Sherbrooke Co., Quebec, 5 Sept. 1974. n, 1 mile NE of Erroll, Coos Co., New Hampshire, 1 Sept. 1976.



referable to *S. cernua* were found abundantly at the type locality, i.e. Mt. Washington, Berkshire County, Massachusetts (ca. 42° 05' N., 73° 27' W.).

The *Spiranthes ochroleuca* plants had distinctly yellowish flowers. (4d, 8d; Royal Horticultural Society colour chart, 1966). The central portion of the lip was deep straw yellow (13c). The *S. cernua* plants had essentially white flowers (155c) with the central portion of the lip at most a very pale creamy-white (6d, 9d).

The yellow-flowered plants were found exclusively in drier sites associated with species characteristic of well-drained soil (e.g. *Plantago lanceolata*, *Rubus flagellaris*, *Hypericum perforatum*, *Pedicularis canadensis*, *Botrychium dissectum* var. *dissectum*, *Vaccinium angustifolium*, *Achillea millefolium*, *Aster ericoides*, *Solidago nemoralis*, *Solidago bicolor*, *Viola fimbriatula*, *Fragaria virginiana*, *Danthonia spicata*, and *Polytrichum* sp.).

The white-flowered plants were found always in wet humic soil with typical species of open mesic to wet sites (e.g. *Prunella vulgaris*, *Ranunculus* spp., *Plantago major*, *Viola* spp., *Lycopus americanus*, *Carex* spp., *Juncus* spp.).

Similar observations of habitat and associates of *Spiranthes ochroleuca* and *S. cernua* have been made consistently. *Spiranthes ochroleuca* is characteristically a colonizer and commonly invades roadcuts and old fields. Large populations may develop in open herbaceous communities, especially in sporadically mowed situations in full sun or occasionally in light shade. It occupies mesic to somewhat xeric sites usually on acidic sandy or rocky soils. Organic mats on acutely drained outcrops are sometimes utilized; there is also some evidence for its occurrence in finer textured soils.

In disturbed sites, *Spiranthes ochroleuca* frequently associates with *S. cernua*, but the two species show distinct moisture preferences. Under the wettest conditions, the latter species occurs alone. In typical roadcut colonies, *S. ochroleuca* is found abundantly on the upper slopes, whereas *S. cernua* occupies ditches. Some mixture occurs on the basal portions of slopes, and *S. cernua* may occur locally about seepages far up the slope. Conversely, a few *S. ochroleuca* may be found in drier situations atop mounds and rocks along the base of the slope.

A phenological difference between *Spiranthes ochroleuca* and *S. cernua* was apparent at Mt. Washington. *Spiranthes ochroleuca* was just coming into its peak of flowering (maximum number of fresh

flowers) when *S. cernua* was slightly past its peak. We have noticed a similar and sometimes more pronounced separation in peak flowering period elsewhere in New England, in Ontario, and in Pennsylvania in those locations where both species occur together.

In summary, the plants of *Spiranthes ochroleuca* at the type locality were the same in general appearance, ecology, and phenology as plants we had come to call *S. ochroleuca* over a wide area of the northeast.

Distinguishing features of *Spiranthes ochroleuca*

Having established the identity of *Spiranthes ochroleuca* on the basis of the original description, the literature in general, the type drawing, and a visit to the type locality, it became obvious that the main source of confusion was *S. cernua*. Other *Spiranthes* species do apparently contribute to the problem, but to a much lesser extent. *Spiranthes laciniata* (type locality: Eustis, Florida) is a taller (to 9.5 dm), more southern coastal plain species with a longer, more loosely spiraling inflorescence and shorter floral bracts. *Spiranthes magnicamporum* Sheviak (1973, type locality: Greene Co., Illinois) occurs mostly to the west of *S. ochroleuca* and is readily distinguished by the absence of basal leaves at flowering time, relatively thick roots (ca. 1 cm), long and narrow perianth parts (ca. 1 cm), and smaller basal calli (ca. 0.5 mm) on the lip. *Spiranthes casei* Catling and Cruise (1974, type locality: Muskoka District, Ontario) occurs mainly to the north of *S. ochroleuca* and differs in having a more loosely flowered spike of relatively smaller flowers with wider lateral sepals, and in its shorter cauline and floral bracts.

Although distinguishing *Spiranthes cernua* was clearly the main problem, it was quite possible to assign most specimens to either *S. ochroleuca* or *S. cernua* and to evaluate their salient characteristics as well as to search for additional ones. Drawings of pickled flowers collected by the authors and examination of living plants over a wide geographical area indicated many characters to be useful to a greater or lesser extent in separating these species.

Spiranthes ochroleuca is most readily recognized in the field by its creamy to ochroleucous flowers which are in sharp contrast to the characteristic white of *S. cernua*. Structurally, they are quite

constant and characteristically distinct from those of *S. cernua* in bearing lateral sepals without any curvature as viewed from above. In *S. ochroleuca* these sepals are commonly appressed to the other floral segments or but slightly spreading and extend stiffly forward, whereas the other segments reflex and curve apically. In *S. cernua*, the lateral sepals nearly always spread slightly from the base and then incurve apically to approach the apices of the dorsal sepal and petals.

The more ascending nature of the lateral sepals and greater separation of the lateral and dorsal sepals in *S. ochroleuca* is clear in Figure 5. The flowers of *S. ochroleuca* also tend to have a greater curvature, both dorsally and ventrally. The ascending nature of the flowers of *S. ochroleuca* and this increased curvature may help to account for the increased separation of the dorsal and lateral sepals as well as for the somewhat larger aperture formed by the basal lip and basal lateral petal. A somewhat greater area of attachment at the top of the ovary, a more downward orientation of the lip stalk, and a more prominent basal hump on the dorsal sepal in *S. ochroleuca* makes these flowers relatively wider basally, and the tube therefore has a greater basal diameter. These features are more or less clear in Figures 5 and 6.

The lips of *Spiranthes ochroleuca* and *S. cernua* differ in some respects and the observed range of variation is illustrated in Figure 7. *Spiranthes ochroleuca* consistently has larger basal calli and exhibits a tendency for the basal parts of the lip to be more gradually tapered resulting in a larger angle of basal curvature (Figures 4c & 7). The basal dilation of the *S. cernua* lip results in a relatively smaller angle of basal curvature and a "hunched shoulders" appearance. The lip of *S. cernua* is often, but not always, more gradually tapered distally, the tapering involving the apical half to third of the lip, whereas in *S. ochroleuca* the tapering is usually limited to the apical quarter of the lip.

In addition, the texture of the lip can be useful in identification. The lip of *Spiranthes ochroleuca* is thick and fleshy, even in softened herbarium material, while in *S. cernua* it is usually membranaceous in such material and only slightly fleshy in fresh condition. The increased fleshiness of the *S. ochroleuca* lip frequently makes the venation difficult to see except through the use of transmitted light. These lip characters must be used with caution

in the determination of dried material. Natural senescence of the flower or poor preservation may sometimes produce apparent basal dilation in lips originally without it, and often alter the fleshy condition to a membranaceous one. Hence, only in well preserved herbarium material should floral characters be used for determination.

As the name implies, the flowers of *Spiranthes cernua* are nodding. This is a nearly constant characteristic and only occasionally do specimens of this species produce horizontal or ascending flowers. These are confined to obviously depauperate, often somewhat etiolated specimens and to a few peculiar forms which show various other abnormalities. In contrast, *S. ochroleuca* exhibits an intrinsic potential for the production of ascending flowers. Often field-grown specimens, especially robust plants in exposed situations, bear nodding basal flowers, but when cultivated under more moderate conditions, such plants in following seasons produce inflorescences with ascending flowers. Certain other characters which are of use in separating *S. ochroleuca* from *S. cernua* are dealt with in the statistical analyses below.

Inflorescences of *Spiranthes ochroleuca* bearing ascending flowers are more slender than those of *S. cernua* bearing nodding flowers of the same size. The comparatively slender inflorescence of ascending flowers in *S. ochroleuca* is distinct in the herbarium and hence can be of use in determination. This would seem to be in opposition to the spike measurements given by Rydberg, but it is difficult to account for the measurements he attributed to *S. cernua*, since only rarely do members of either of these species exhibit such slender inflorescences. In fact the ranges given by Rydberg are much too restrictive. Both species exhibit a similar range in inflorescence diameter, although *S. ochroleuca* averages somewhat smaller than *S. cernua*.

The more slender appearance of the *Spiranthes ochroleuca* inflorescence is often enhanced by a higher angle to the parastichy in this species, which contributes a more open aspect to the inflorescence than in most plants of *S. cernua*. Especially in small specimens, the insertion of flowers in *S. ochroleuca* may be in a rather evident spiral with the vertically superposed flowers so removed as to eliminate obvious orthostichies. Such a situation is known in *S. cernua* only in a few forms from restricted parts of its

range. Robust specimens of *S. ochroleuca*, especially in exposed sites, however, commonly exhibit inflorescences as dense and obviously ranked as those of *S. cernua*.

The floral bracts of *Spiranthes ochroleuca* are generally somewhat longer than in northeastern material of *S. cernua*. They tend to be narrower and more gradually tapered. In *S. cernua* they are often widest at a point approximately one third the distance from the base to the apex; above this point they taper abruptly to a long, rather aristate tip. The longer, more acuminate bracts of *S. ochroleuca* together with a more open inflorescence make the inflorescence of this species appear greener and more "leafy." These features of the floral bracts are best evaluated in qualitative terms because they exhibit a good deal of overlap.

Foliar characters may also serve to distinguish these species. Under favorable conditions leaves of *Spiranthes ochroleuca* are sessile to short-petiolate, arcuate-spreading, oblanceolate to elliptical, canaliculate, and of a curious rough-flexible texture. A few may be borne on the lower portion of the stem. In *S. cernua*, in contrast, leaves are more typically petiolate, often notably so, ascending, linear-lanceolate to oblanceolate, conduplicate, and membranaceous. They are only rarely borne on the stem. Variation toward *S. ochroleuca* in all of these features is sometimes seen, however.

Both authors have maintained plants referable to *Spiranthes ochroleuca* and *S. cernua* in cultivation under uniform conditions. With the few exceptions noted above, all distinctive characteristics including flower colour, morphology, and phenology have been maintained. Significantly, uniform cultural conditions have been found to enhance the expression of distinctive characters over their manifestation in the field. Correlation of the characteristics of individuals in the field, under cultivation, and in the pressed condition has been of great importance in assessing the potential phenotypes and variability in these species.

Geographical Distribution

Figure 8 shows the distribution of *Spiranthes ochroleuca* based on collections of the authors and readily determinable material from a number of herbaria. It is interesting to compare this distribution with the ranges determined by Swamy (1948). Swamy showed the "sexual race of *S. cernua*" to be confined to the northeast from New England south through New York and Pennsylvania. This compares

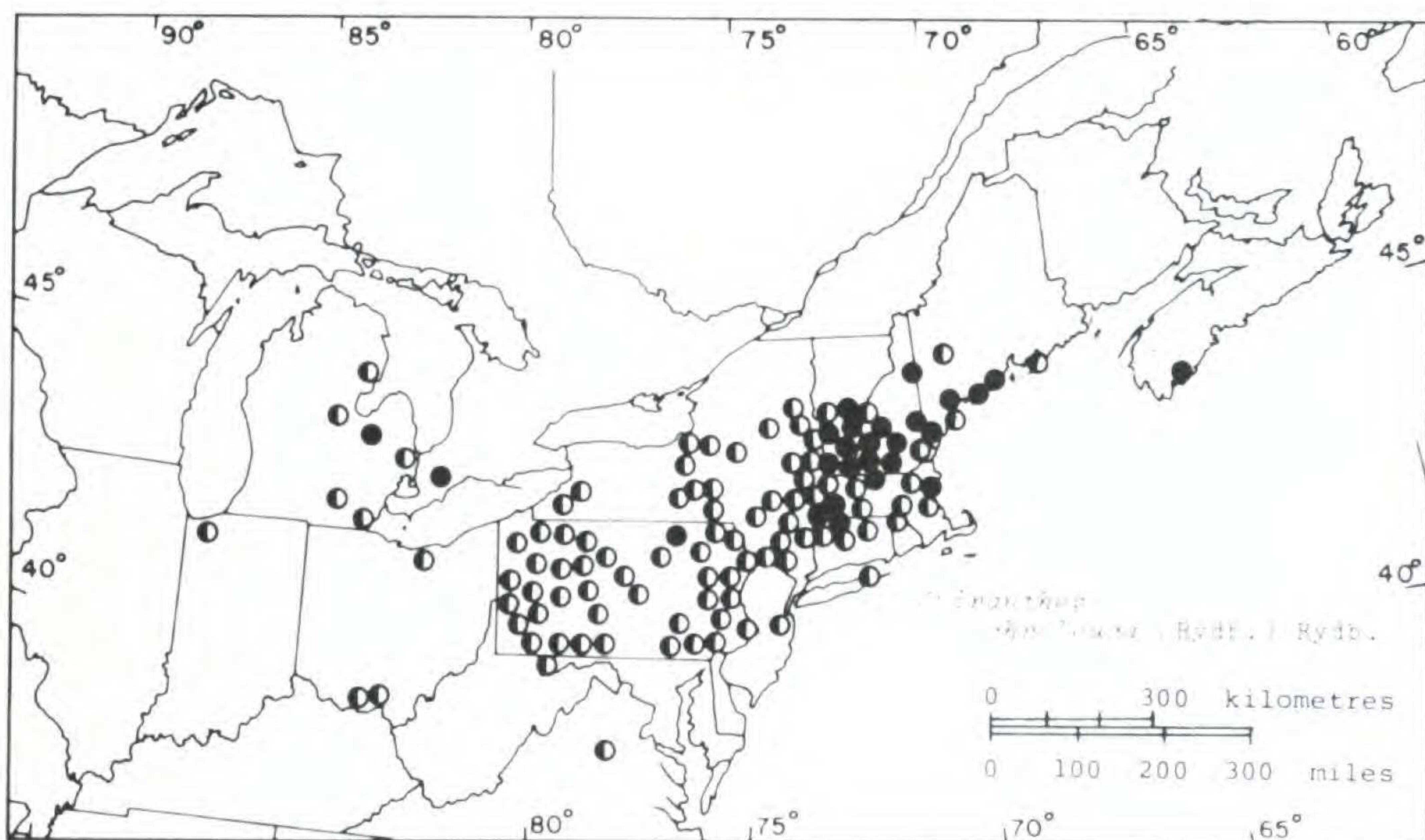


Figure 8. The distribution of *Spiranthes ochroleuca* (Rydb.) Rydb. in the northeast based on personal collections of C. J. Sheviak and P. M. Catling (solid dots) and on well preserved and easily assigned herbarium specimens (half dots).

closely with our map of the distribution of *S. ochroleuca*. Swamy found a much wider distribution of the “asexual and intermediate races of *S. cernua*” to the north, west, and south corresponding with our determination of the range of *S. cernua*. Swamy’s races were based on reproductive mode and embryo number, whereas our map reflects study of morphological characters.

Seeds, chromosomes, and pollen

It should be clear from this discussion that typical *Spiranthes ochroleuca* is readily distinguished from most *S. cernua* when living material is being considered; greater difficulty is encountered with dried material. In the herbarium some specimens cannot be satisfactorily placed through consideration of any commonly cited gross morphological characters. This situation drove Ames to conclude that the only reliable character was embryo number. Correll (1950) commented on the ultratechnical nature of this character and, indeed, it is undesirable to be forced to such extremes. However, our experience indicates that it does provide a clear distinction between the species: *Spiranthes ochroleuca* pro-

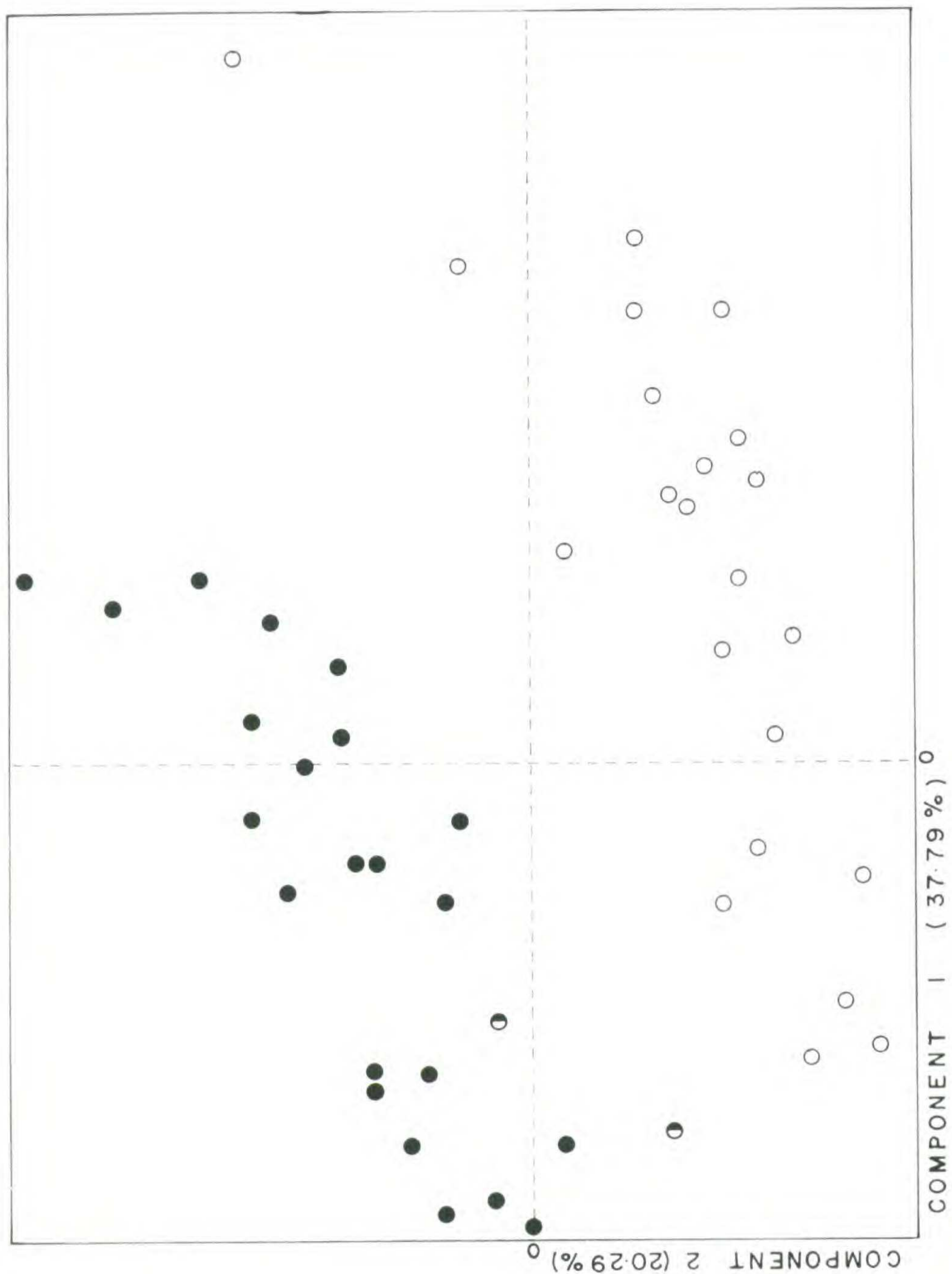


Figure 9. A 2-dimensional view of the position of 22 pickled flower specimens of *S. ochroleuca*, 22 of *S. cernua* and 3 "intermediates", on principal components 1 and 2 extracted from the matrix of correlations among 24 characters measured in material from the type locality, Mt. Washington, Mass. Open circles = *S. ochroleuca*, darkened circles = *S. cernua* and half-darkened circles = "intermediates".

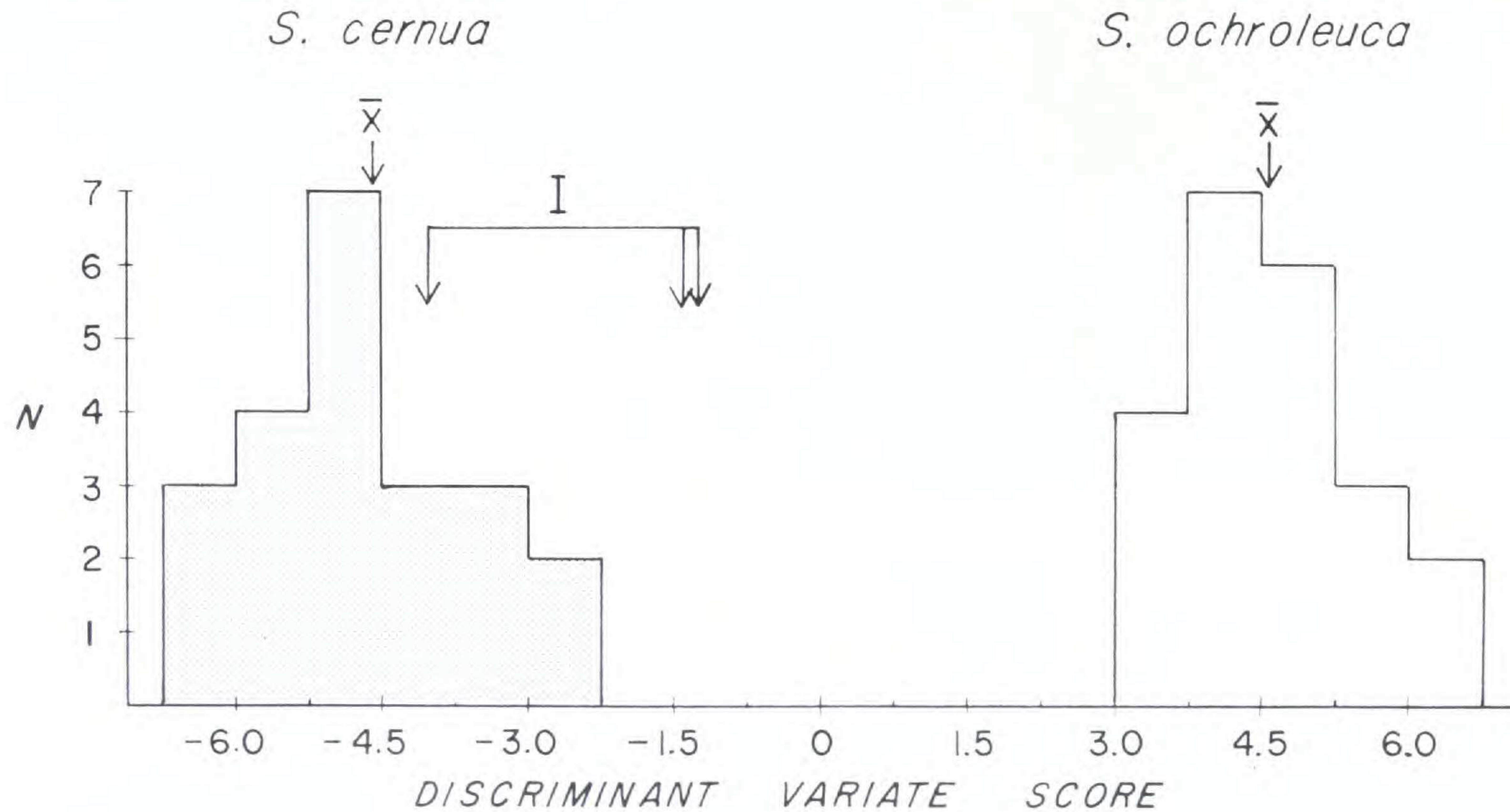


Figure 10. Histograms of discriminant scores of 22 pickled flower specimens of *S. ochroleuca* and 22 of *S. cernua*. The position of 3 apparent intermediates (I) is indicated. The plot is based on the "best" discriminant function incorporating 7 floral characters derived in stepwise fashion from 24 (see Table 1). For *S. ochroleuca* the group mean ($\bar{x}$) is 4.65 and the standard deviation of scores is 0.86. For *S. cernua* the group mean ($\bar{x}$) is -4.65 and the standard deviation is 1.12.

duces strictly monoembryonic seeds, whereas different forms of *S. cernua* yield varying percentages of polyembryonic seeds. Swamy has shown sexually reproductive plants to produce monoembryonic seeds and polyembryony to result from adventitious embryony. Detailed work on the *S. cernua* complex (Sheviak, unpubl.) has shown diploids to be sexually reproductive, whereas all polyploids exhibit apomictic potential. In the present study, we have obtained strictly diploid counts ($2n = 30$) on specimens determined as *S. ochroleuca*, and only polyploid counts ($2n = 60$ or rarely 45) on *S. cernua* (see Table 3). Hence embryo number appears to be an important character which serves to separate the diploid *S. ochroleuca* from the polyploid *S. cernua*.

Care must be taken with seed characters, however, since some obligately apomictic races of *Spiranthes cernua* exhibit a low percentage of polyembryony. A casual examination is therefore insufficient. Observation of polyembryony requires some patience. If herbarium material is being studied, seeds should be softened before examination, as this greatly aids resolution of closely overlapping embryos. Additionally the lack of understanding of the mechanism regulating reproductive mode in *Spiranthes* dictates caution, and seed characters are best used in conjunction with others.

Swamy (1948) reported pollen degeneration in asexual *Spiranthes cernua* and noted normal behavior in the sexual race, i.e. *S. ochroleuca*. Pollen abortion appears to be influenced by the environment; in our greenhouse studies we have observed this phenomenon and in addition irregularities of stipe and disc formation to be associated with high ambient temperatures. *Spiranthes ochroleuca* and various other species exhibit the same anomalies as *S. cernua*. Although different races of *S. cernua* show differing susceptibility to such conditions and the causes of the phenomenon are unknown and deserve further study, it appears that pollen degeneration is of little taxonomic significance.

Statistical analysis of flower morphology

In Principal Components Analysis (Figure 9) flowers from *Spiranthes ochroleuca* determined on the basis of flower colour,

general aspect, and habitat cluster together. None of the *S. cernua* clusters with *S. ochroleuca* and vice-versa. This clustering, based on a matrix of correlations among 24 features of flower morphology, is very important since it demonstrates clearly that these taxa, previously separated on the basis of various qualitative characters may also be separated quantitatively on the basis of floral structure alone.

The means, standard deviations, and units of the various characters are given in Table 1. The most powerful discriminating characters are the length of the stigmatic surface, length and width of lateral petal, length and width of anther sac, length of sepal, angle of curvature of lip from basal stalk, length of basal calli, separation of dorsal and lateral sepal, and the angle of basal curvature of the lip "shoulders," which measures basal dilation. Some of these are the same characters that were found to be most significant in separating the two species over a broad geographic area.

The Discriminant Functions Analysis (Figure 10) clearly separates *Spiranthes ochroleuca* from *S. cernua*. The "intermediate" plants in both PCA and DFA are more closely associated with *S. cernua* than *S. ochroleuca*, reflecting a morphological similarity that was evident even in the field. This clustering of the intermediates with the tetraploid *S. cernua* is a predictable result of dilution of the *S. ochroleuca* genome in allopolyploids; the entirely comparable results of the analysis of dried material, which included known triploids (see below), supports this hypothesis.

Statistical analysis of dried material

Collection locality, number of specimens, and chromosome numbers are provided in Table 3. The specimens represent a wide geographical area; in the case of *Spiranthes ochroleuca*, 23 percent are topotypes. Of the *S. cernua* specimens, 35 percent are from outside the principal range of *S. ochroleuca* in the northeast. Units, means, standard deviations, and DFA character weights are given in Table 2.

Again in PCA (Figure 11), *Spiranthes ochroleuca* specimens determined as such on the basis of flower colour, various qualitative characters, and habitat formed a fairly well-defined cluster distinct

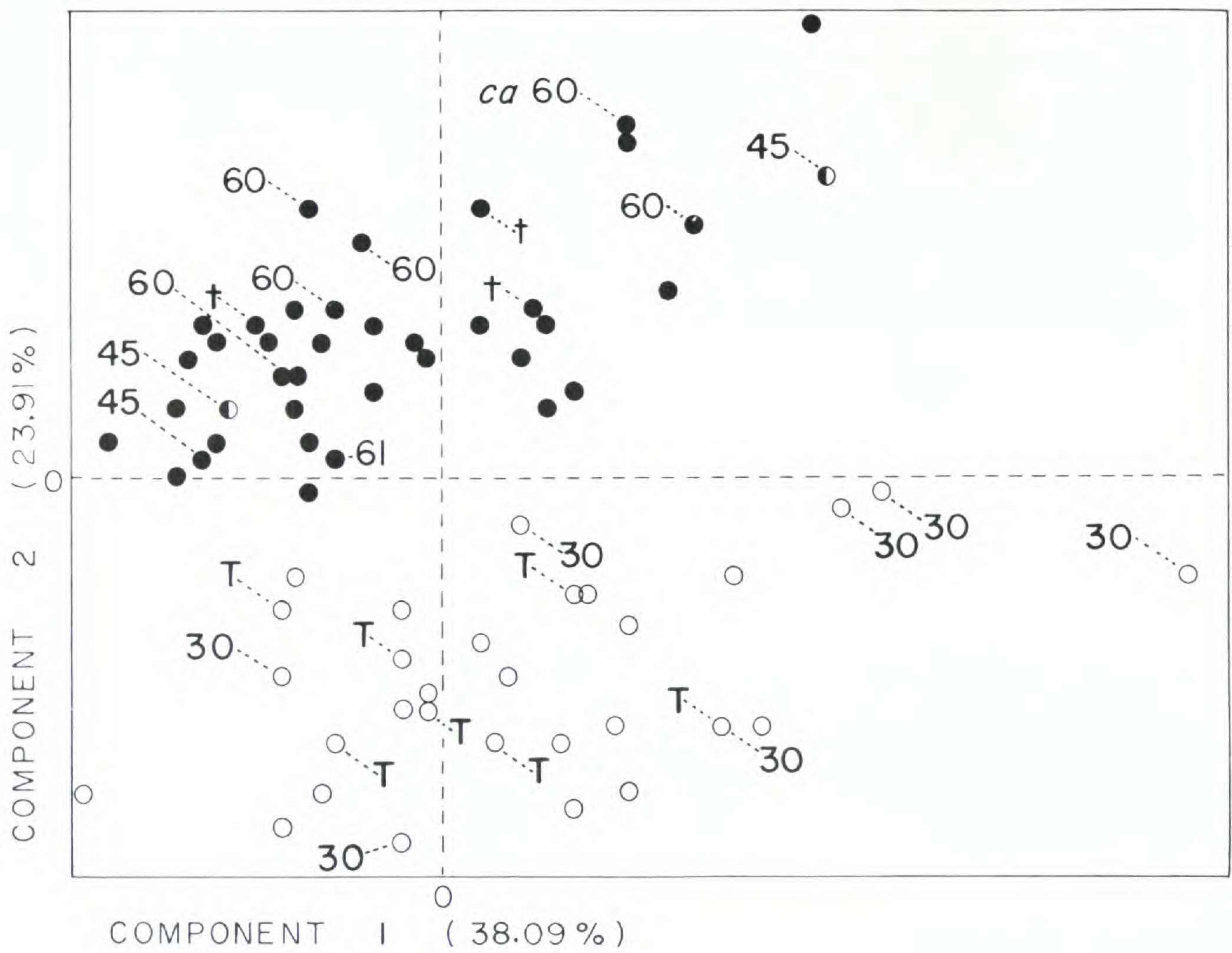
from the *S. cernua* cluster. All diploid plants are located in the *S. ochroleuca* cluster while triploids and tetraploids are confined to the *S. cernua* cluster. Topotypes of *Ibidium incurvum* cluster with *S. cernua* and topotypes of *S. ochroleuca* cluster with plants referable to *S. ochroleuca* from elsewhere. Based on this morphological analysis, *I. incurvum* is not distinguishable from *S. cernua*, and *S. ochroleuca* from the type locality corresponds to *S. ochroleuca* over a broad geographical area.

Since the clusters are formed on the basis of quantitative morphology alone, and correspond to nominant *Spiranthes ochroleuca* and *S. cernua*, it is suggested that dried material can be correctly determined without weighting characters. We have been convinced of this for some time, and indeed our distribution map is based on the determination of herbarium material without character weighting.

The most useful characters in determining dried specimens were found to be the distance of separation of the dorsal and lateral sepals, and the curvature of the lip from the basal stalk. The length of the lowest floral bract and length of midstem bract are also useful. However, there is moderate overlap in all of these characters as might be expected with pressed and dried material. Certain characters that have already been discussed qualitatively can be evaluated in quantitative terms for the dried material in Table 2. One that has not been discussed previously is the tendency toward a somewhat larger ovary in *S. cernua* flowers at anthesis, a condition probably related to the early development of adventitious embryos (Swamy, 1948).

Flower colour, general appearance, habitat, and PCA on quantitative morphology have established the two species *Spiranthes ochroleuca* and *S. cernua* in the dried material. Using these determined groupings it is possible to find and evaluate the best means of discrimination using DFA. The results of two discriminant

Figure 11. A 2-dimensional view of the position of 30 dried specimens referable to *S. ochroleuca*, 37 referable to *S. cernua* and 2 indeterminates, on principal components 1 and 2 extracted from the matrix of correlations among 11 characters measured in dried material from throughout the northeastern U.S. and adjacent Canada. Open circles = *S. ochroleuca*, darkened circles = *S. cernua*, half-darkened circles = indeterminates. Chromosome counts are shown for certain OTU's and topotypes of *Ibidium incurvum* (t) and *Spiranthes ochroleuca* (T) are also identified.



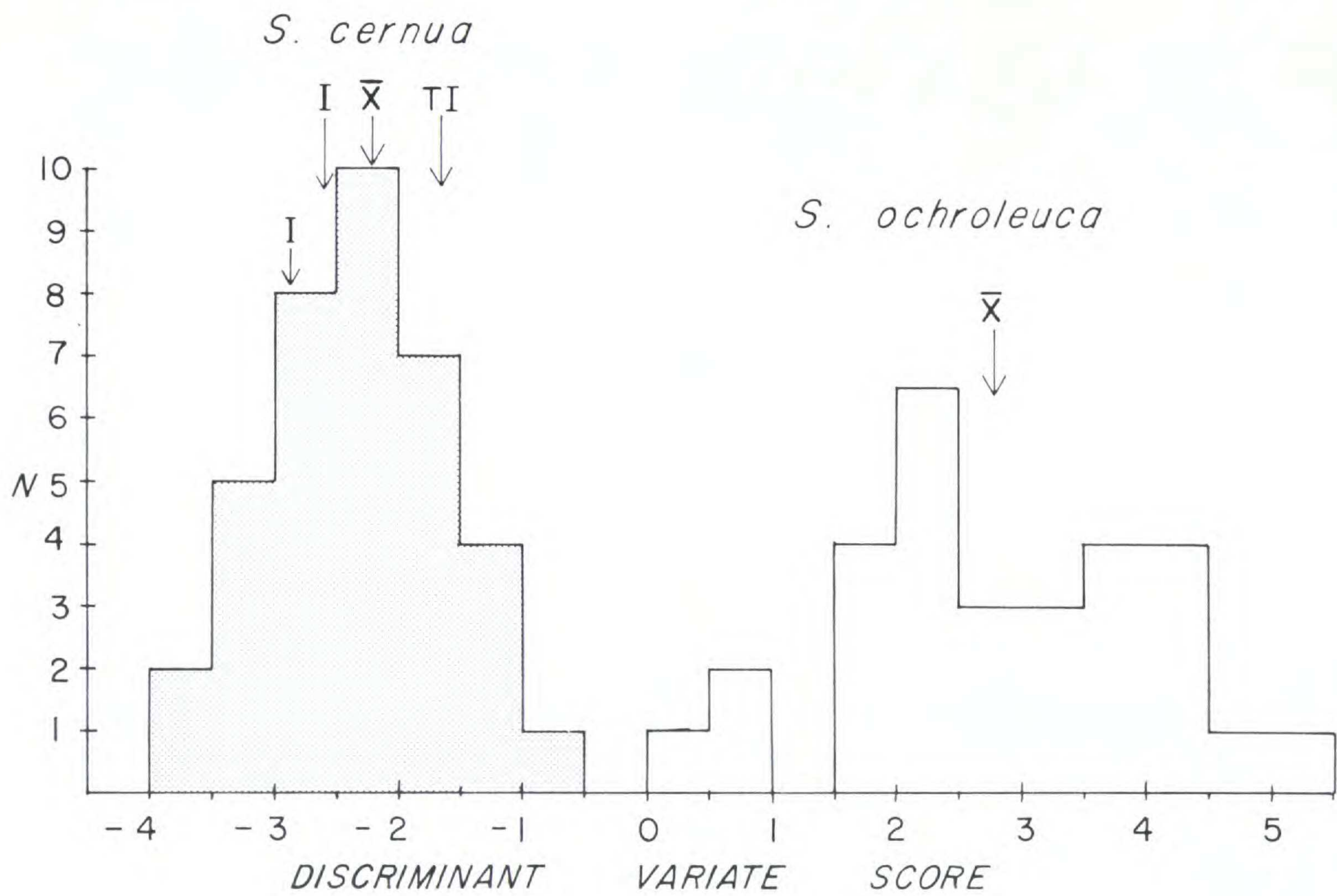
function analyses are shown in Figures 12 and 13. The former employs all eleven measured characters. The histogram of discriminant scores shows the scores to be distributed bimodally. The separation is more clear than in the PCA, as is to be expected with character weighting. No specimens are "misdetermined" (i.e., are placed differently than their flower colour, general appearance, morphology, and habitat would indicate). In the second analysis based on only four characters, separation is less dramatic but discrimination is complete. This function has the advantage of being more convenient for determination of herbarium material. It has, however, a disadvantage in relying more heavily on the separation of the dorsal and lateral sepals. If the flowers were withered when pressed or were very tightly pressed, this character may be difficult to use.

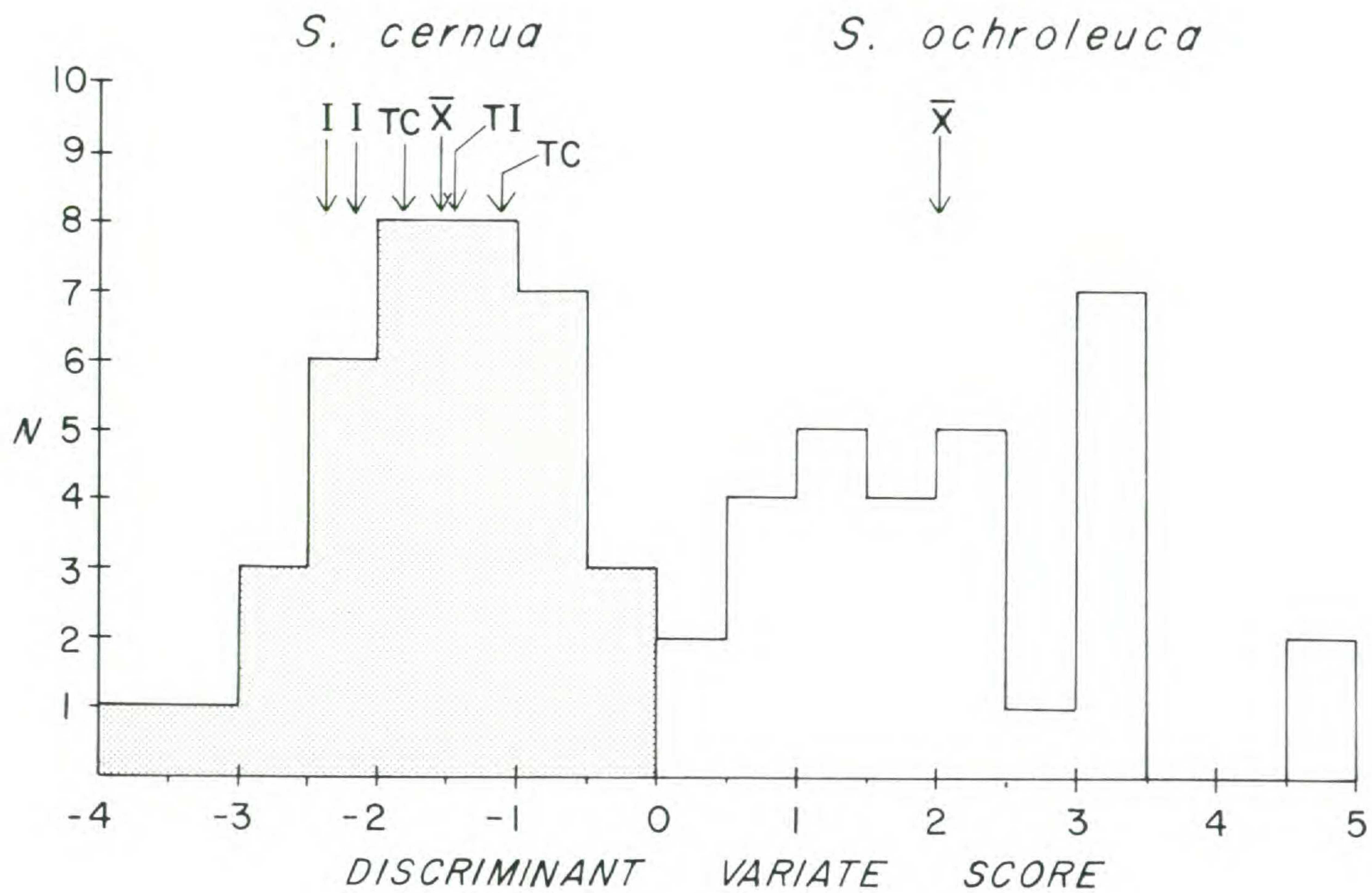
A limited set of measurements was available for the type of *Spiranthes cernua* (LINN 1056.9) enabling the use of the second discriminant function. The resultant scores place the two plants representing the type of *S. cernua* in with the group representing *S. cernua* as defined by recent American authors (Figure 13). In both DFA histograms an isotype of *Ibidium incurvum* (CM 5603) falls into the *S. cernua* group, again suggesting that the former name be placed in synonymy with the latter. Also in both of the DFA histograms the triploids fall within the *S. cernua* group as they did in unweighted analysis (Figure 11). Interestingly, two of the three triploids could not be determined in the field while one was determined as *S. cernua*. This suggests the possible occurrence of unidirectional gene flow from *S. ochroleuca* to *S. cernua*, a situation which will require detailed experimental work for proper verification.

CONCLUSIONS

This study indicates that *Spiranthes ochroleuca* is a diploid, sexual species morphologically, ecologically, and to some extent

Figure 12. Histograms of discriminant scores of 30 dried specimens referable to *S. ochroleuca* and 37 referable to *S. cernua*. The plot is based on a discriminant function using all 11 characters measured (see table 2). The indeterminates, later found to be triploids, are positioned ($I = -2.60, -2.84$) as well as the isotype of *Ibidium incurvum* ($TI = -1.68$). For *S. ochroleuca*, the group mean ($\bar{X}$) is 2.78 and the standard deviation of scores is 1.24. For *S. cernua*, the group mean ($\bar{X}$) is -2.25 and the standard deviation is 0.750.





phenologically distinct from the polyploid, facultatively apomictic *S. cernua*. In contrast to the widespread *Spiranthes cernua*, *S. ochroleuca* exhibits a distinctive restricted distribution, occurring primarily in the northeast and becoming very rare and local westward. These differences clearly distinguish *S. ochroleuca* from *S. cernua* and justify specific rank. Topotype collections made by the authors (*C.J. Sheviak & J. Hart 1076*, 21 September 1976; and *P.M. Catling 831c*, 10 September 1976), for which data on habitat, flower colour, morphology, etc. are available, may be found at AMES, TRT, and CAN.

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Figure 13. Histograms of discriminant scores of 30 dried specimens of *S. ochroleuca* and 37 of *S. cernua*. The plot is based on a discriminant function using 4 of 11 characters (see table 2) that are easily and consistently measurable. The positions of the two plants representing the type of *Spiranthes cernua* (TC= -1.17, -1.83), two indeterminates later found to be triploids (I=-2.19, -2.24) and the isotype of *Ibidium incurvum* (TI=-1.47) are shown. For *S. ochroleuca* the group means ($\bar{x}$) is 2.01 and the standard deviation of scores is 1.18. For *S. cernua* the group mean ($\bar{x}$) is -1.63 and the standard deviation is 0.83.

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